NOTES ON THE MARINE ALGAE OF THE BERMUDAS. 2. SOME RHODOPHYTA, INCLUDING *POLYSIPHONIA TONGATENSIS* AND A DISCUSSION OF THE *HERPOSIPHONIA SECUNDA/TENELLA* COMPLEX[1,2]

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ABSTRACT — Eight marine red algae are reported from the Bermuda islands for the first time (*Balliella pseudocorticata*, *Champia parvula* var. *prostrata*, *Diplothamnion jolyi*, *Grallatoria reptans*, *Heterosiphonia crispella* var. *laxa*, *Polysiphonia tongatensis*, *P. flaccidissima* and *Wrangelia argus*) and three others represent poorly known taxa from the islands (*Halydictyon mirabile*, *Polysiphonia exilis*, and *P. sphaerocarpa*). A lectotype is designated for *Champia parvula* var. *prostrata* L.G.Williams. A unique, net-forming *Hydrolithon farinosum* from deep water is recorded and its structure described, and transfer of a variety of *Fosliella farinosa* is made to *Hydrolithon farinosum* as *H. farinosum* var. *chalicodictyon* (W.R.Taylor) C.W.Schneid. *et* Searles comb. nov. A precise explanation of the repeating branching pattern of offshore Bermuda specimens of *Herposiphonia secunda* highlights the taxonomic confusion associated with this pantropical species, and *Polysiphonia tongatensis* is shown to be the correct name for Atlantic and Pacific Ocean specimens previously attributed to *P. eastwoodiae*.

RÉSUMÉ — La présence de huit algues rouges marines est signalée pour la première fois aux Bermudes (*Balliella pseudocorticata*, *Champia parvula* var. *prostrata*, *Diplothamnion jolyi*, *Grallatoria reptans*, *Heterosiphonia crispella* var. *laxa*, *Polysiphonia tongatensis*, *P. flaccidissima* et *Wrangelia argus*) ainsi que celle de trois autres très mal connues dans ces îles (*Halydictyon mirabile*, *Polysiphonia exilis* et *P. sphaerocarpa*). Un lectotype est désigné pour *Champia parvula* var. *prostrata* L.G.Williams. Un *Hydrolithon farinosum* de profondeur, tout à fait particulier, formant un réseau, a été récolté et sa structure décrite ; la combinaison *H. farinosum* var. *chalicodictyon* (W.R.Taylor) C.W.Schneid. *et* Searles comb. nov. est proposée, à partir d'une variété de *Fosliella farinosa*. Une explication précise des différents types de succession de motifs répétés de ramification existant chez les spécimens d'*Herposiphonia secunda* des Bermudes récoltés au large, éclaicit la confusion taxinomique qui régnait jusqu'alors pour cette espèce pantropicale, et *Polysiphonia tongatensis* apparaît comme le nom correct à attribuer aux spécimens des océans Atlantique et Pacifique rapportés jusqu'à présent à *P. eastwoodiae*. (Traduit par la Rédaction)

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KEY-WORDS: Bermuda, *Herposiphonia*, *H. secunda*, *Hydrolithon*, *Polysiphonia*, *P. tongatensis*, *P. eastwoodiae*, Rhodophyta, new record, taxonomy, new combination.

INTRODUCTION

Much has been learned about the benthic marine algae of Bermuda since they were first collected during the 1850s (for a summary of the investigations leading to the known present-day flora, see Schneider & Searles, 1997). Despite Bermuda's remote location approximately 1000 km east of the Carolinas in North America, the islands have in fact gained over geologic time a sizable marine flora with the majority of species arriving from Florida and the Caribbean Sea *via* the dispersal route of the Florida Current anf Gulf Stream (Searles & Schneider, 1987). There are, by our accounting, about 412 reasonably reliable species of seaweeds presently reported in Bermuda (221 Rhodophyta, 66 Phaeophyta, 118 Chlorophyta, 7 Chrysophyta), with several others in need of taxonomic investigation. This total reflects species that have been verified by collections during the 20th century and includes only 32 more than reported for Bermuda more than a quarter century ago (Taylor & Bernatowicz, 1969). Several species reports by Kemp (1857), Rein (1873), Dickie (1874), Hemsley (1884), Murray (1888, 1889) remain unsubstantiated and therefore questionable in the flora (and are not included in the above total), but we have recollected one of their early records, *Polysiphonia exilis* Harv., growing on offshore reefs as well as in the midlittoral zone with the similar *P. howei* Hollenb.

Perhaps due to Bermuda's relatively young age and small size (Collins & Hervey, 1917), only seven species of those with type localities in the archipelago (44 species, 1 subspecies, 9 varieties, 1 form) are still considered endemic, including one we recently described, *Antithamnionella bermudica* C.W. Schneid. (Schneider & Searles, 1997). In the present paper, we add six additional species to the flora as well as two varieties not previously reported, and verify some taxa reported previously as uncommon or rare. From deep offshore waters, we illustrate and describe a unique reticulate *Hydrolithon*, and discuss its relationship with *H. farinosum* var. *chalicodictyon* (W.R. Taylor) C.W. Schneid. *et* Searles comb. nov. Collections of *Herposiphonia secunda* (C. Agardh) Ambronn from deep water allow us to precisely define its branching topology and to relate pattern considerations to the taxonomic discussion associated with this species and *H. tenella* (C. Agardh) Ambronn.

MATERIALS AND METHODS

Most of the collections were made on two cruises of the R/V *Seahawk* in August, 1983 and June, 1985 around the Bermudas (for dive site data, see Searles & Schneider, 1987; for collection methods, see Schneider & Searles, 1997). Liquid preserved specimens were mounted in 20 % Karo® corn syrup, 1 % aniline blue and 1N HCl in a ratio of 97:1:2 on glass microscope slides. Dried herbarium specimens were cut and stained with 1 % aniline for 2 minutes directly on the paper, soaked for 5 minutes in 45 % glacial acetic acid and then the papers with specimens were mounted in 50 % Karo on glass slides. Drawings were made using a Zeiss camera lucida and photomicrographs were taken on Kodak T Max-100 professional film using an Olympus BH-2 microscope equipped with S Plan Apochromatic objective lenses and an Olympus camera. Vouchers of these collections are deposited in DUKE or the first author's personal herbarium (CWS), and duplicates of some species have been sent to AHFH, C, GALW, HBFH, MICH, NFLD, NY, US, and the Bermuda Aquarium, Natural History Museum and Zoo [BAMZ]. Herbarium abbreviations follow Holmgren *et al.* (1990) and standard forms of author names follow Brummitt & Powell (1992).

OBSERVATIONS

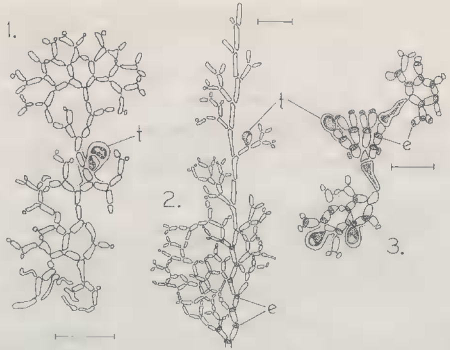
CORALLINALES, CORALLINACEAE

Hydrolithon farinosum (J.V.Lamour.) Penrose & Y.M.Chamb. 1993: 295
Figs 1-3

Basionym: *Melobesia farinosa* J.V. Lamour. 1816: 315
Type locality: Unspecified site, Mediterranean Sea.
Collections: Bermuda-*CWS/RBS* 85-1-34, 5 June 1985, south of Sinky Bay, 32° 13.0" N, 64° 50.5′ W, depth 31 m; *CWS/RBS* 85-5-5, 7 June 1985, north of Pilchard Dicks, northwest of Somerset Is., 32° 23.6′ N, 64° 55.0′ W, depth 32 m; *CWS/RBS* 85-15-34, 13 June 1985, northeast of Great Head, St Davids Is., 32° 22.8′ N, 64° 36.4′ W, depth 30-34 m; *CWS/RBS* 85-18-9, 15 June 1985, south of Christian Bay, southwest end Bermuda Is., 32° 13.2′ N, 64° 50.7′ W, depth 27-40 m, on *Lobophora*.

Remarks: We have found epiphytic, loosely affixed coralline crusts in deep water which form beautiful nets (Figs 1, 2) reminiscent of *Rhododictyon* and *Hydrodictyon*. Although these specimens are vegetative and lack diagnostic germination discs (Irvine & Chamberlain, 1994), they are in part bistratose, contain terminal, divided trichocytes and most probably are representative of the *Fosliella*-state of *Hydrolithon* as described by Penrose & Chamberlain (1993). At maturity, the trichocytes are divided into basal and hair-bearing portions (Fig. 1), typical for *Hydrolithon* (Chamberlain, 1983, as *Fosliella*). We find our deep-water specimens best attributed to *H. farinosum* based upon their characteristic triangular propagules (Fig. 3), similar to those illustrated as *Fosliella farinosa* (J.V. Lamour.) M. Howe by Coppejans (1978, 1983) and Cormaci & Furnari (1988) from the Mediterranean Sea. Afonso-Carrillo (1989) found the absence of diagnostic germination discs to be correlated with vegetative reproduction, and that propagules were an important means of reproduction/dispersal in the '*Fosliella*-state of *Hydrolithon*.' Interestingly, we have not found any crusts which bear propagules, only reticula germinating from them.

In the thin Bermuda crusts, epithallial cells do not consistently form on all specimens (Fig. 1), often forming only on the older portions of the reticulum (Fig. 2). Oblique terminal divisions of hypothallial cells ultimately divide and rebranch, connecting up with cells from adjacent rows and forming meshes roughly pentagonal or hexagonal in design (Fig. 1). This reticulum is more elaborate than the wavy-row patterned crust exhibited by ***Hydrolithon farinosum* var. *chalicodictyon* (W.R.Taylor) comb. nov.** [Basionym *Fosliella farinosa* var. *chalicodictya* W.R.Taylor, *Smithson. Misc. Coll.* 98: 10, figs 13,14, pl. 1, figs 1-3 (1939)], where central portions of curved hypothallial cells are laterally conjoined leaving lacunae between non-connected portions of spreading rows (Coppejans, 1976, 1983). None of our reticulate specimens show these H-shaped cell connections. Elsewhere in Bermuda, we have also collected classic *H. farinosum* var. *chalicodictyon* in deep water (*CWS/RBS* 85-19-14, 15 June 1985, southwest of Long Bar, west of High Point, Bermuda Is., 32° 13.5′ N, 65° 01.3′ W, depth 30-34 m) and this variety



Figs 1-3. *Hydrolithon farinosum*. All scale bars = 50 µm. Fig. 1. Habit of an entire young reticulate hypothallium with a single divided trichocyte (t). Fig. 2. Spreading edge portion of crust with a percurrent axis bearing epithallial cells (e) in lower portions and an undivided trichocyte distally. Fig. 3. Triangular propagule generating new reticula which quickly produce epithallia and bear trichocytes.

bears little resemblance to our reticulate crusts. *H. farinosum* var. *chalicodictyon* often develops unconsolidated growth at the extremes of the crust, and this is also true of the reticulate Bermuda specimens. In our collections, occasional cell rows become percurrent, exhibiting an alternate branching pattern with meshes forming to the right and left of the nearly straight cell rows (Fig. 2), giving the edge of the crust a less compact appearance. These alternating nets off the percurrent axes eventually fill in as shown by larger reticula with straight axes running through them.

Such thin crusts as we have described with abundant trichocytes are typical of warm-water and high light intensity environments (Irvine & Chamberlain, 1994). Certainly, our specimens at depths as great as 40 m are growing in diminished light intensities despite the clarity of midsummer warm Bermuda waters. Even though the habit of our *Hydrolithon* crusts is apparently unique, Irvine & Chamberlain (1994) have found that it "now seems unnecessary formally to name sporadically occurring, unconsolidated growth forms as taxonomic entities," due to the morphological variability not only within species but within populations. At this point, we choose simply to illustrate the characteristics of our offshore reticulate *H. farinosum*, as they appear to display a singular growth form not previously known in the Corallinales.

RHODYMENIALES, CHAMPIACEAE

Champia parvula (C.Agardh) Harv. var. *prostrata* L.G.Williams *in* Pearse & L.G.Williams 1951: 155

Type locality: New River Inlet, Onslow Bay, North Carolina, western Atlantic.
Collections: Bermuda-*CWS/RBS* 85-23-14, ⊕, 19 June 1985, The Spit, northeast of Little Head, St Davids Is., 32° 22.4′ N, 64° 38.5′ W, depth 1-12 m, on *Galaxaura obtusata* (J. Ellis *et* Sol.) J.V. Lamour.; *CWS* 96-5-11, ⊕, 3 July 1996, Bailey's Bay, Bermuda Is., 32° 20.8′ N, 64° 43.4′ W, depth 3-4 m, on *Dictyota neglecta* Hörnig *et* Schnetter.

Remarks: The Bermuda specimens are distinctly flattened except in the most basal portions, segments are obviously constricted at the nodes, and globose tetrahedral sporangia (50-70 µm in diameter) are densely clustered in several adjoining segments, conforming to *Champia parvula* var. *prostrata* previously reported only from deep water in the southeastern United States (Schneider & Searles, 1991). Williams (1951) never designated a holotype for his new variety. The only original material cited in the protologue found in DUKE or US, the repositories of the bulk of Williams' collections, is DUKE Acc. No 00969 [1], and this specimen is herein designated as the lectotype according to Art. 9.2 of the ICBN (Greuter *et al.*, 1994). Both the lectotype and Bermuda collections are very small and epiphytic, similar in size and axial dimensions to *C. minuscula* A.B.Joly & Ugadim, but they lack the small clustered cortical cells and terete axes of that species (Joly *et al.*, 1965). The compressed axes are reminiscent of *C. compressa* Harv. and *C. vieillardii* Kütz., two species with taxonomic distinctions pointed to in the recent literature (Millar, 1990; Wynne, 1995). Unlike the lectotype and Bermuda plants here attributed to *C. parvula* var. *prostrata*, among other things *C. compressa* is pinnately branched and *C. vieillardii*, with its segments much broader than long, lacks constrictions at the nodes.

CERAMIALES, CERAMIACEAE

Balliella pseudocorticata (E.Y. Dawson) D.N. Young 1981: 94
Fig. 4

Basionym: *Antithamnion pseudocorticatum* E.Y. Dawson 1962: 20
Type locality: San Lorenzo Channel, La Paz, Baja California del Sur, Pacific Mexico.
Collection: Bermuda-*CWS/RBS* 85-5-14, 85-5-24, 7 June 1985, north of Pilchard Dicks, northwest of Somerset Is., 32° 23.6′ N, 64° 55.0′ W, depth 32 m.

Remarks: On the basis of his phylogenetic analysis of the Ceramiaceae, Athanasiadis (1996) removed *Balliella* from the subfamily Ceramioideae, placing it in the tribe Delesseriopseae rather than in the Antithamnieae as proposed by Huisman & Kraft (1984). Bermuda plants are slightly larger (to 7 mm), have little rhizoidal cortication and somewhat smaller axial cells than the protologue from the Pacific Ocean (Dawson, 1962).

1. *LGW*, 22 July 1949, Onslow Co., North Carolina, off New River Inlet on *Amphiroa brasiliana* Decne. [= *A. beauvoisii* J.V. Lamour.], depth 6 m, cystocarpic.

Figs 4-9. Bermuda Ceramiales. Fig. 4. *Balliella pseudocorticata*, habit. Scale bar = 100 µm. Figs 5-6. *Grallatoria reptans*. Fig. 5. Stilt-walking habit. Scale bar = 0.5 mm. Fig. 6. Polysporangia on upper portion of whorl-branch. Scale bar = 50 µm. Figs 7-9. *Wrangelia argus*. Fig. 7. Axial portion of upright indeterminate axis showing habit of determinate whorl-branches. Scale bar = 100 µm. Fig. 8. Habit of indeterminate axis with unilateral development of secondary indeterminate axes from basal cells of whorl-branches. Scale bar = 0.5 mm. Fig. 9. Stilt-walking habit with attaching digitate rhizoids. Scale bar = 150 µm. Fig. 10. *Herposiphonia secunda*. Habit of a developing tip. Scale bar = 200 µm.

but otherwise these specimens are best identified with *B. pseudocorticata*. At their greatest, axial cells are 65 µm in diameter and 190 µm long. Abaxial gland cells are occasionally paired with a smaller second one as noted in Baja California and Galapagos Is. specimens (Young, 1981). Like the only other known plants from the Atlantic Ocean (Hoek, 1978, as *Bakothamnion curassavicum* C.Hoek; Ballantine & Wynne, 1986; Hanisak & Blair, 1988), the Bermuda specimens are vegetative which makes the species determination problematic (Huisman & Kraft, 1984).

Diplothamnion jolyi C.Hoek 1978: 51

Type locality: Klein Piscadera, Curaçao, Lesser Antilles, Caribbean Sea.
Selected collections: Bermuda-*CWS/RBS* 83-4-27, 5 Aug. 1983, east of St Catherine's Point, 32° 23.9′ N, 64° 34.3′ W, depth 18-21 m; *CWS/RBS* 83-5-34, 6 Aug. 1983, southeast of Southampton Is. and Gurnet Rock, 32° 19.9′ N, 64° 39.3′ W, depth 20-28 m; *CWS/RBS* 83-6-7, 6 Aug. 1983, due south of Soldiers Pt, St Davids Is., 32° 19.8′ N, 64° 39.3′ W, depth 47-50 m; *CWS/RBS* 85-2-16, 6 June 1985, southwest of Chub Heads, due west of Elys Harbor, 32° 17.6′ N, 65° 01.0′ W, depth 19 m; *CWS/RBS* 85-15-17, 13 June 1985, northeast of Great Head, St Davids Is., 32° 22.8′ N, 64° 36.4′ W, depth 30-34 m; *CWS/RBS* 85-18-11, 15 June 1985, south of Christian Bay, southwest end Bermuda Is., 32° 13.2′ N, 64° 50.7′ W, depth 27-40 m.

Remarks: All of the abundant specimens of *Diplothamnion jolyi* thus far obtained in Bermuda are epiphytic on other deep-water algae and are vegetative. Sexual plants of this species were reported for the first time from the Canary Islands (Sansón & Reyes, 1994), and they supported Gordon's (1972) provisional placement of the genus in the Sphondylothamnieae. Aside from the earlier reports from the Caribbean Sea and the Canaries, this species has recently been reported from Atlantic Florida (Hanisak & Blair, 1988), the Key Largo marine sanctuary (Bucher *et al.*, 1990) and for the first time in the Pacific from Hawaii (Hodgson & Abbott, 1992).

Grallatoria reptans M.Howe 1920: 560
Figs 5, 6

Type locality: Great Ragged Is., Bahamas, western Atlantic.
Collection: Bermuda-*CWS/RBS* 83-5-38, ⊕, 6 Aug. 1983, southeast of Southampton Is. and Gurnet Rock, 32° 19.9′ N, 64° 39.3′ W, depth 20-28 m.

Remarks: Sporangial plants of this classic "stilt-walker" (Fig. 5) contain both tetrahedral tetrasporangia and polysporangia (Fig. 6). Although this is the first report of polysporangia for *Grallatoria reptans*, these could possibly be the "ovoid, globose or pyriform densely granular cysts 60-150 µm diameter occasional" mentioned in the protologue by Howe (1920). The polysporangia are slightly larger than tetrasporangia and often appear granular, but the largest only reach 30 µm in diameter and 48 µm long. Although Abbott (1976) placed this species in *Callithamniella*, Wynne & Ballantine (1985) offered substantive characters for retaining *Grallatoria* as a separate genus. The superficially similar *Callithamniella tingitana* (Schousb. *ex* Bornet) Feldm.-Maz. was also recently reported from deep Bermuda offshore waters (Schneider & Searles, 1997).

Bermuda represents the third known site for *Grallatoria reptans* outside the Caribbean Sea with earlier reports from eastern Florida (Hanisak & Blair, 1988) and the

Canary Islands (Sansón, 1994). As is true for other small and creeping, epiphytic algae which are easily overlooked, or those that reside in only deeper water where collections are infrequent at best, *G. reptans* probably has a much wider distribution than is presently known at least in the Atlantic Ocean if not in other tropical seas.

Wrangelia argus (Mont. *in* Webb & Berthel.) Mont. 1856: 444
Figs 7-9

Basionym: *Griffithsia argus* Mont. *in* Webb & Berthel. 1841 [1839-1842]: 176
Type locality: Canary Islands, eastern Atlantic.
Collections: Bermuda — *CWS/RBS* 83-5-1, 6 Aug. 1983, southeast of Southampton Is. and Gurnet Rock, 32° 19.9′ N, 64° 39.3′ W, depth 20-28 m; *CWS/RBS* 83-7-18, 7 Aug. 1983, south of Warwick Long Bay, Bermuda Is., 32° 13.8′ N, 64° 48.5′ W, depth 40-44 m; *CWS/RBS* 85-1-10, 5 June 1985, south of Sinky Bay, 32° 13.0′ N, 64° 50.5′ W, depth 31 m; *CWS/RBS* 85-18-8, 15 June 1985, south of Christian Bay, southwest end Bermuda Is., 32° 13.2′ N, 64° 50.7′ W, depth 27-40 m.

Remarks: It is surprising that prior to this report *Wrangelia argus* had not been collected in Bermuda given its range in the western Atlantic from Florida to Brazil and extensive distribution in the Gulf of Mexico and Caribbean (Taylor, 1960; Joly & Cordeiro, 1962). The deep-water specimens reported here have all been found as velvety turfs to 1 cm high on *Lobophora variegata* (J.V.Lamour.) Womersley *ex* E.C.Oliveira. Their main axes are to 230 µm in diameter although most often closer to 160 µm and each axial cell bears 3-4 (-5) determinate whorl-branches mostly developed to three orders of branching (Fig. 7). The more diminutive and also ecorticate *W. dumontii* (E.Y.Dawson) I.A.Abbott from the Pacific regularly produces three whorl-branches from a node, and *W. argus* from the Caribbean, produces four, or occasionally five, whorl-branches (Abbott, 1979). Erect indeterminate axes arise unilaterally from the basal cells of whorl-branches issued from extensive prostrate axes (Fig. 8), similar to those reported for *W. argus* from St Croix by Abbott (1979). The tips of most indeterminate branches slightly curve towards the side of indeterminate branches which are issued from them. As is typical for the species, some, but not all, Bermuda *W. argus* specimens develop delicate, loose cortication around nodal regions by wrapping the delicate, curved determinate whorl-branchlets issued from whorl-branch basal cells around the axes (see Børgesen, 1916, fig. 125). Many nodes are completely naked. Prostrate axes are attached by multicellular rhizoids cut off from basal cells of whorl-branches, developing digitate tips upon contact with the host (Fig. 9). Therefore, *W. argus* has a similar spreading habit not only to *W. dumontii* , but also to *Grallatoria reptans* with which it grows near Gurnet Rock (coll. 83-5).

The presence of 3 whorl-branches on some or all nodes of certain plants adds to the variability in habit and axial dimensions that we have found for *Wrangelia argus* in DUKE and MICH, and we choose to retain our vegetative specimens under this epithet. Two larger, corticated species in the genus, *W. bicuspidata* Børgesen and *W. penicillata* (C. Agardh) C. Agardh, have previously been reported from Bermuda (Collins & Hervey, 1917; Taylor, 1960).

DASYACEAE

Halydictyon mirabile Zanardini 1843: 52

Type locality: Adriatic Sea, Mediterranean.
Collections: Bermuda-*CWS/RBS* 83-8-24, 7 Aug. 1983, Jacks Flats, east of St Georges Is., 32° 23.1′ N, 64° 38.0′ W, depth 15-18.5 m; *CWS/RBS* 85-15-24, 13 June 1985, northeast of Great Head, St Davids Is., 32° 22.8′ N, 64° 36.4′ W, depth 30-34 m.

Remarks: Although Taylor (1928) noted this species as having been reported for Bermuda in his treatise on Florida marine algae, we can find no early records or specimens to substantiate this claim, including a search in MICH, the repository of Taylor's extensive collections. However, at a later time, Taylor (1961) attributed some "very scarce" net-forming Bermuda specimens to *Halydictyon mirabile* amidst the treatment of his new genus *Rhododictyon*. We too, have collected *H. mirabile* in Bermuda, but only from a few deep-water locations. Bucher & Norris (1995) summarized the recent distributional reports of this species in the western Atlantic.

Heterosiphonia crispella (C.Agardh) M.J.Wynne var. *laxa* (Børgesen) M.J.Wynne 1985b: 87

Basionym:*Heterosiphonia wurdemannii* (Bailey *ex* Harv.) Falkenb. var. *laxa* Børgesen 1919: 327
Type locality: St Croix, Virgin Islands, Lesser Antilles, Caribbean Sea.
Selected collections: Bermuda-*CWS/RBS* 83-4-26, 5 Aug. 1983, east of St Catherine's Point, 32° 23.9′ N, 64° 34.3′ W, depth 18-21 m; *CWS/RBS* 85-2-39, 6 June 1985, southwest of Chub Heads, due west of Elys Harbor, 32° 17.6′ N, 65° 01.0′ W, depth 19 m; *CWS/RBS* 85-9-18, 8 June 1985, northeast of Northeast Breakers, 32° 31.2′ N, 64° 39.6′ W, depth 37 m; *CWS/RBS* 85-20-5, 15 June 1985, southwest of Long Bar, Bermuda Is., 32° 13.7′ N, 65° 01.0′ W, 24-27 m; *CWS* 92-3-2, ⊕, 19 June 1992, Walsingham Pond, 32° 20.7′ N, 64° 42.8′ W, depth 0-1 m; *CWS* 92-5-4, 21 June 1992, Horseshoe Bay, 32° 15.0′ N, 64° 49.2′ W, in drift; *CWS* 96-2-9, ⊕, 1 July 1996, Harrington Sound, east side of Flatts Inlet bridge, 32° 19.4′ N, 64° 44.2′ W, depth 1-3 m, on tunicates; *CWS* 96-4-14, 2 July 1996, Coot Pond, Achilles Bay, St Georges Is., 32° 23.2′ N, 64° 40.66′ W, depth 1 m.

Remarks: Børgesen (1919, as *Heterosiphonia wurdemanni*) remarked that although Falkenberg (1901) had speculated that var. *laxa* might be a "deep sea form", he had found both var. *typica* and var. *laxa* in shallow and deep-water collections. We have collected *H. crispella* var. *laxa* from just below the low water mark to 37 m offshore corroborating Børgesen's finding in the Caribbean Sea. This variety has been widely reported in the literature for the western Atlantic since Taylor (1960, as *H. wurdemanni* var. *laxa*) (Guimarães *et al.*, 1981; Schneider & Searles, 1991; Bucher & Norris, 1995), and its presence in Bermuda adds to its widespread distribution. Interestingly, *P.B.-A.* No 2097 (Collins *et al.*, 1916), distributed as *H. wurdemanni* from Harrington Sound, Bermuda, prior to the erection of Børgesen's new variety, is also representative of *H. crispella* var. *laxa* (*P.B.-A.* 597 from Key West, Florida represents typical var. *crispella* [Collins *et al.*, 1899a]). Schlech & Abbott (1989) have suggested that the varieties of *H. crispella* are unnecessary based upon continuous variation in some Hawaiian specimens, but we will

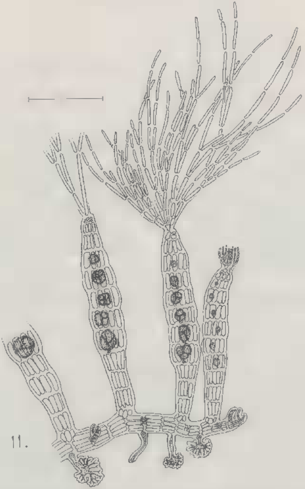


Fig. 11. *Herposiphonia secunda.* Habit of the growing tip of a tetrasporangial specimen. Scale bar = 3 mm.

continue to use the infraspecific entities which are separable in the western Atlantic until a definitive study is made.

RHODOMELACEAE

Herposiphonia secunda (C.Agardh) Ambronn 1880: 197
Figs 10, 11

Basionym: *Hutchinsia secunda* C. Agardh 1824: 149
Type locality: Mediterranean Sea.

Collections: Bermuda-*CWS/RBS* 85-1-23, ⊕, 5 June 1985, south of Sinky Bay, 32° 13.0′ N, 64° 50.5′ W, depth 31 m, on *Dictyota*; *CWS/RBS* 85-5-6, ⊕, 7 June 1985, north of Pilchard Dicks, northwest of Somerset Is., 32° 23.6′ N, 64° 55.0′ W, depth 35 m, on *Stypopodium*.

Remarks: *Herposiphonia secunda* is a species which has had considerable taxonomic confusion and controversy over time (Hollenberg, 1968c; Wynne, 1985a). Some workers consider *H. tenella* (C. Agardh) Ambronn a form of *H. secunda*, while others continue to recognize two separate species, though not always for the same reason (see Wynne, 1985a; Schneider & Searles, 1991). Branching pattern, including the arrangement of determinate (d) and indeterminate (i) laterals as well as the occurrence of unbranched or "naked" nodes (n), has been classically used to differentiate the two (Taylor, 1960), but variation in this character within populations of both has been demonstrated (Morrill, 1976). The basic branching pattern for *H. tenella* (and the most common pattern for other species in the genus) involves a dorsal branch from every segment in a sequence of determinate and indeterminate branches in a repetitive pattern of d/d/d/i. Determinate branches are alternately displaced to the left (l) and right (r) with the most distal branch on the same side as the next distal indeterminate branch, thus in actuality the pattern is precisely ld/rd/ld/li/rd/ld/rd/ri or 8 periaxial segments from base to apex before repeating the entire sequence (Ambronn, 1880; Falkenberg, 1901; Børgesen, 1918; Schneider & Walde, 1992, fig. 1). All species of *Herposiphonia*, including *H. tenella*, exhibit some variation in branching pattern and these differences are usually mentioned in species' descriptions.

Herposiphonia secunda has been described as having a basic branching pattern with 1-4 naked nodes interrupting the pattern of determinate and indeterminate branches (Ambronn, 1880; Taylor, 1960; Hollenberg, 1968c). Bermuda specimens here assigned to *H. secunda* have a fairly consistent branching pattern of a determinate branch preceded distally by one rudimentary, or at least somewhat developed, indeterminate branch and then one naked node. Examination of several specimens shows that although d/i/n (base to apex) is the most common pattern for *H. secunda* offshore in Bermuda, occasional axes have a greater or lesser number of naked nodes. Precisely, Bermuda specimens have a 6-repeating pattern of ld/li/n/rd/ri/n, clearly following the left and right sequence of Mediterranean plants illustrated by Falkenberg (1901, pl. 3, fig. 11). This d/i/n/d/i/n pattern has subsequently been illustrated by several workers (Price & Scott, 1992, fig. 61b; Børgesen, 1918, upper fig. 289, as *H. tenella*; Joly, 1965, fig. 648; Abbott & Hollenberg, 1976, fig. 668, as *H. tenella* f. *secunda*), but Børgesen (1920, lower fig. 429) shows the 6-repeating pattern for this species sequenced differently (d/n/i/d/n/i). In some portions of certain Bermuda specimens, the branching abruptly becomes repetitive d/i/d/i lacking naked nodes and similar to the basic pattern illustrated for *H. xaymaca* V.J. Chapm. (1963, fig. 132c), a species distinguished from other *Herposiphonia* species mostly on this character. Specimens of *H. xaymaca* should be carefully checked for naked nodes and the 6-segment repeating pattern shown for *H. secunda*, as it may well be a further variant of this morphologically variable taxon.

Interestingly, Ambronn (1880, Pl. IV, fig. 17 [II]) demonstrates a base to apex branching pattern for *Herposiphonia secunda* mostly of 8-segment repeating units of d/i/n/n/d/i/n/n, similar to what he shows for *H. tenella* where determinate branches replace naked nodes (Pl. IV, fig. 17[I]). Taylor (1960) states that *H. secunda* has "axes with an indeterminate branch or a rudiment of one usually preceding each [determinate] branchlet, these originating from every fifth or sixth node," thus a 10- or 12-segment repeating pattern. All of the above repeating patterns of varying numbers of segments are currently included under the pantropical *H. secunda*. It is important to carefully study the general branching pattern of *Herposiphonia* specimens/species as work using L-systems computer software to model branching topology has demonstrated the necessity of precise pattern rules to define relationships of species and genera in the dorsiventral Rhodomelaceae, the group to which it belongs (Schneider & Walde, 1992).

Deep-water Bermuda specimens of *Herposiphonia secunda* have stout segments on determinate branches, 0.5-0.9 times as long as broad (Fig. 10), a characteristic noted by Falkenberg (1901) and Hollenberg (1968c) for plants from the Mediterranean (type locality), as well as illustrated by others from a variety of locales (e.g., Børgesen, 1918, lower fig. 289, as *H. tenella*; Dawson, 1963; Abbott & Hollenberg, 1976, as *H. tenella* f. *secunda*; Cribb, 1983, as *H. tenella* f. *secunda*). Tetrasporangia on our plants are formed in short to long spiraled series in distal portions of determinate axes (Fig. 11). This spiraled development has been clearly demonstrated for plants referred to this species from other places including the type locality, the Mediterranean Sea (Børgesen, 1930, fig. 45a; Dawson, 1963, pl. 140, fig. 2; Coppejans, 1983, pl. 246, fig. 2).

DESCRIPTION: Because of the great variation among descriptions of this taxon throughout the world, a thorough description of plants of *Herposiphonia secunda* from Bermuda seems appropriate:

Plants epiphytic and creeping, brownish red, attached by distally and ventrally issued, unicellular, pit-connected rhizoids, these often with digitate tips; prostrate indeterminate axes 80-130 µm in diameter with 8 periaxial cells, segments 0.5-3.0 times as long as broad, mostly bearing a repetitive branching pattern of a determinate branch followed by a naked node and then an indeterminate primordium or branch; determinate branch tips slightly upturned, with young determinate branches curling towards them and mostly overtopping; erect indeterminate branches mostly remaining rudimentary, those developing following the pattern of the main axis; determinate branches simple, slightly tapering to the base, 0.5-1.4 mm tall, 60-95 µm in diameter, 12-14 (-18) segments long, each segment 0.5-0.9 times as long as broad, terminally bearing 2-4 times dichotomously branched trichoblasts, becoming deciduous on older determinates, remaining rudimentary on others; tetrasporangia globose, 60-110 µm in diameter, one per segment, formed in a continuous or broken spiraled series of 10-12, swelling the fertile branch to 185 µm in diameter at maturity giving it a nodulose appearance, in distal portions of determinate branches.

***Polysiphonia tongatensis* Harv. *ex* Kütz. 1864: 14, pl. 41, figs a-d**
Figs 12-14

= *Polysiphonia senticulosa sensu* Mrs E.Snyder *in* Collins, Holden & Setchell 1899b, *P.B.-A.* 638a, b (not *P. senticulosa* Harv. 1862: 169)
= *P. eastwoodiae* Setch. *et* N.L.Gardner 1930: 161 [as *P. eastwoodae*]
= *P. snyderiae* Kylin 1941: 35, pl. 12, fig. 34 [as *P. snyderae*]
= *P. aquamara* I.A.Abbott 1947: 212
= *P. mollis sensu* Hollenb. 1961: 359, 1968a: 69 [not fig. 43] (not *P. mollis* Hook. f. *et* Harv. *in* Harv. 1847: 43)
= *P. mollis* Hook. f. *et* Harv. var. *tongatensis* (Harv. *ex* Kütz.) Hollenb. *ex* P.C. Silva, Meñez & R.L.Moe 1987: 70
Type locality: Tonga, Friendly Is., south Pacific.
Collections: Bermuda-*CWS/RBS* 85-3-14, ♀ , ⊕, 6 June 1985, southwest of Chub Heads,

Figs 12-19. Bermuda *Polysiphonia* species. Figs 12-14. *P. tongatensis*. Fig. 12. Apex of tetrasporangial specimen. Scale bar = 250 µm. Fig. 13. Apex of a spermatangial specimen. Scale bar = 200 µm. Fig. 14. Cystocarps. Scale bar = 250 µm. Fig. 15. *P. exilis*, habit showing dorsally issued upright axes and ventral rhizoids. Scale bar = 0.5 mm. Figs 16-18. *P. flaccidissima*. Fig. 16. Prostrate axis habit with dorsally issued upright axes and ventral rhizoids. Scale bar = 200 µm. Fig. 17. Tip segments showing the origin of lateral branches. Scale bar = 100 µm. Fig. 18. Apex of a spermatangial specimen. Scale bar = 100 µm. Fig. 19. *P. sphaerocarpa*, cystocarp. Scale bar = 100 µm.

32° 17.6′ N, 65° 02.0′ W, depth 27 m; *CWS/RBS* 85-23-19, ⚥, ⊕, 19 June 1985, The Spit, northeast of Little Head, St Davids Is., 32° 22.4′ N, 64° 38.5′ W, depth 1-12 m; *CWS* 96-4-12, ♀, ♂, ⊕, 2 July 1996, Coot Pond, Achilles Bay, St Georges Is., 32° 23.2′ N, 64° 40.66′ W, depth 1 m.

Remarks: We have collected plants in Bermuda which conform to recent Atlantic and Pacific records of *Polysiphonia eastwoodiae* Setch. *et* N.L.Gardner (1930; type locality, Guadalupe Is., off Pacific Baja California), a large, erect, basally affixed species with dramatic tapering from base to apex. However, we have also discovered confusing taxonomy and nomenclature associated with the binomial *P. eastwoodiae*, as highlighted in various publications of G.J. Hollenberg. In his monographic treatment of *Polysiphonia* from Pacific Mexico, Hollenberg (1961, p. 359) listed *P. eastwoodiae* along with *P. snyderiae* as heterotypic synonyms of *P. mollis*, later adding *P. aquamara* from Hawaii (1968a). Subsequent publications from the Pacific Ocean followed Hollenberg's lead in referring '*eastwoodiae*' specimens to *P. mollis* (e.g., Meñez, 1964; Abbott & Hollenberg, 1976; Hollenberg & Norris, 1977). But when Womersley (1979, p. 477) pointed out that branches in the Harvey type (Tasmania) and his own South Australian material of *P. mollis* arose in the axils of trichoblasts, unlike the known cicatrigenous branching in *P. eastwoodiae*, it was obvious that there were at least two similar Pacific entities based upon this well-accepted branching criterion for *Polysiphonia*.

Other specimens that some workers considered, at least for a time, best placed in *Polysiphonia mollis* along with *P. eastwoodiae* were certain collections attributed to *P. tongatensis* (Hollenberg, 1961; Hollenberg & Norris, 1977, but carefully excluding the original Tonga material of *P. tongatensis*), including a potential new variety from Guadalupe Is. (unnamed due to its fragmentary nature, Setchell & Gardner, 1930) and specimens from Japan (Segi, 1951). Prior to Womersley's (1979) clarification of *P. mollis*, Hollenberg (1968a, p. 69) proposed a new status for *P. tongatensis* as *P. mollis* var. *tongatensis* (Harv. *ex* Kütz.) Hollenb., but without proper validation [Art. 33 ICBN, Greuter *et al.*, 1994; this taxon was validated in the Silva *et al.* Philippines catalogue (1987, p. 70) and would correctly be cited as *P. mollis* var. *tongatensis* (Harv. *ex* Kütz.) Hollenb. *ex* P.C. Silva, Meñez et R.L. Moe]. When Kützing (1864) described *P. tongatensis* Harvey ined., he did not illustrate or describe the origin of branching necessary for later workers to show conspecificity with *P. mollis*. Neither did Grunow (1874) when he discussed the similarities of these two species and compared Graeffe's specimens with Harvey's from Tonga. Since then, there have been conflicting reports on branch origins. For Japanese plants attributed to *P. tongatensis*, Segi (1951, p. 207) reported that "branchlets [arise] in patent axils," whereas Børgesen (1954, p. 38) unequivocally stated that his Mauritian specimens showed branches replacing trichoblasts. Both authors report looking at Setchell material of *P. tongatensis* from Tahiti (UC 261338), yet neither mention any observations directly on type material.

In an attempt to clarify the confusion, we have observed the two sets of Harvey's (1857) Friendly Is. Exsiccata (Tonga, No 14, *Polysiphonia tongatensis* Harv.) housed in MICH, each consisting of two cards (ultimately originating from two different sources, the Brooklyn Institute Museum and the collection of A.R. Young). We assume that the collection Kützing cited in the protologue (1864, p. 14) is the exsiccata housed in Leiden and represents the holotype (Rec. 9A.4 ICBN, Greuter *et al.*, 1994). Actually, this specimen (L 941.240-178) containing the notation "Friendly Is., Herb. Sonder" on the label in Kützing's hand is apparently a portion of the holotype "Tonga, No 14" presumably now housed in MEL, the repository of the bulk of Sonder's herbarium (two Harvey specimens exist in MEL [T. Entwisle, pers. comm.]). Thus, all of the other widely distributed Harvey Friendly Is. duplicates, "14, Tonga," including those we have observed in MICH, are considered isotypes (Art. 9.3). We have found no evidence of anything other than cicatrigenous branching in these specimens that were observed with trichoblasts intact, and as discussed below, find no vegetative or reproductive characters to differentiate this species from *P. eastwoodiae*. Thus, we can substantiate earlier claims of the conspecificity of the antecedent *P. tongatensis* and its heterotypic synonym, *P. eastwoodiae*. Furthermore, because *P. tongatensis* lacks branches arising from the basal cells of intact trichoblasts, based upon mode of branching alone, it cannot be an infraspecific taxon of *P. mollis*.

Polysiphonia tongatensis, like *P. eastwoodiae*, has been widely reported in the Indo-Pacific (Tsuda & Wray, 1977; Silva *et al.*, 1987; South & Kasahara, 1992; Yoshida *et al.*, 1995; Silva *et al.*, 1996). *P. eastwoodiae* has also been reported in the Atlantic Ocean from Venezuela (Kapraun *et al.*, 1983), Brazil (Yoneshigue & Villaça, 1986) and Mexico (Aguilar Rosas *et al.*, 1992). Kapraun *et al.* (1983) compared their Atlantic plants with the AHFH isotype of *P. eastwoodiae* as well as Pacific Mexico specimens of *P. mollis sensu* Hollenberg (1961, 1968a). The Bermuda specimens represent the first report of this species complex in the Atlantic north of South America. Adding our Bermuda collections of *P. tongatensis* to the above reports from the Atlantic makes it seems unlikely that the occurrence of this species in the Caribbean/Atlantic represents a new arrival via the Panama Canal as considered by Kapraun *et al.* (1983, as *P. eastwoodiae*); rather *P. tongatensis* appears to be a taxon with a broad geographic distribution in tropical/subtropical seas, similar to many other species in the genus (see following account of *P. sphaerocarpa* Børgesen).

Our specimens from Coot Pond were epiphytic on other algae in a tangled mat which included *Jania adhaerens* J.V.Lamour., *Centroceras clavulatum* (C.Agardh *in* Kunth) Mont. *in* Durieu, *Ceramium cimbricum* H.E.Petersen *in* Rosenv., *C. flaccidum* (Kütz.) Ardiss., *Spyridia hypnoides* (Bory *in* Bél.) Papenf., *Chondria polyrhiza* Collins *et* Herv., and *Polysiphonia flaccidissima* Hollenb. on weathered volcanic rock in the bay. Offshore *P. tongatensis* was found growing on *Laurencia obtusa* (Huds.) J.V. Lamour. and *Cladophora longicellulata* C.Hoek. This primarily erect species is characterized by subdichotomous branches replacing trichoblasts in the spiral sequence at the apices (Fig. 12). Trichoblasts are issued one per segment in a 1/4 spiral and are tufted at the tips, later becoming deciduous, leaving persistent scar cells. Børgesen (1954) reports that trichoblasts in his Mauritian specimens are issued in a 1/4 spiral, but only on every other segment, not conforming with other observations for *P. tongatensis*. Bermuda specimens arise from rhizoidal holdfasts and reach nearly 2 cm in height, and thus, although agreeing in mode of attachment, are considerably smaller than the type material (4-6 cm) and other Pacific collections (5-8 cm, Kylin, 1941, as *P. snyderiae*; to 8 cm, Abbott, 1947, as *P. aquamara*). Main axes can become secondarily attached from proximally issued rhizoids, occasionally more than one per cell, which are cut off from one or more of the four periaxial cells in each segment. The plants are somewhat rigid below and the axes taper dramatically from base to apices (see Yoneshigue & Villaça, 1986, fig. 10, as *P. eastwoodiae*); axial segments are 310-350 µm in diameter just above the only slightly flared basal attachments, in median sections they are 150-220 µm in diameter further tapering to 30-50 µm in diameter below the apices. The four isotypes of *P. tongatensis* show segments 300-350 µm in diameter near the base and tapering upwards to similar dimensions as in the Bermuda material. In the protologue of *P. eastwoodiae* (Setchell & Gardner, 1930) and other Pacific accounts, basal segments are 350-400 µm in diameter; those reported from the Atlantic as *P. eastwoodiae* are 200-300 µm, but otherwise the vegetative characteristics fit *P. tongatensis* well. Two other primarily erect species that show similar marked decreases in diameter over their axes include *P. gorgoniae* Harv. and *P. binneyi* Harv., only the latter being known in Bermuda (Taylor, 1960). Both of these species, however, have branch development in the axils of trichoblasts (Kapraun, 1979, fig. 22; Kapraun *et al.*, 1983, fig.4). Unlike *P. ferulacea* Suhr *ex* J. Agardh, a species with similar branch and rhizoid development also known from Bermuda, *P. tongatensis* has segments in median portions which are approximately 1.5-3 times as long as broad (Figs 13, 14). *P. ferulacea* has stout segments throughout (one or less times as long as broad) and much shorter spindle-shaped branches which would not be confused with *P. tongatensis*.

Tetrasporangia in the Bermuda specimens are formed in short, occasionally broken, spiral series in upper portions of the branches, noticably swelling the segments at maturity (Fig. 12). One of the MICH Harvey specimens shows immature tetrasporangia in similar subapical series. Kajimura (1979, p. 120, fig. 4) reports subterminal, tightly bound, spiraled-series of tetrasporangia in ultimate branches for *Polysiphonia tongatensis* from Japan. But because of the reported branching ontogeny of the specimens reported by Segi (1951), the reports of *P. tongatensis* from Japan are to held in question until further investigation is made. In Bermuda, a single sporangium is formed per segment, and they range from slightly elongate to globose and 40-80 µm in diameter basically with the smaller tetrasporangia in the offshore collections and the larger ones in shallow water. The range of tetrasporangial sizes is smaller than the protologue description of *P. eastwoodiae* (90-110 µm, Setchell & Gardner, 1930) but slightly larger than other collections from the Pacific (50-60 µm, Young & Kapraun, 1985, as *P. eastwoodiae*; 60-70 µm, Hollenberg, 1961, as *P. mollis*) and Atlantic (50-62[-92] µm, Yoneshigue & Villaça, 1986, as *P. eastwoodiae*). This appears to be a somewhat variable character and given the newly proposed geographic range for *P. tongatensis*, this is hardly surprising. The spermatangial sori on one isotype card are remarkably well preserved, showing their formation on basal cells of trichoblasts, at times being subtended by persistent trichoblasts. They range from 22-50 µm in diameter and 90-200 µm although some of the largest ones seem to have been squashed apart in pressing. In Bermuda, spermatangial sori are similarly formed and are 25-65 µm in diameter and 120-210 µm long with or without a single vegetative tip cell (Fig. 13), a variable feature also seen in the male Tonga specimen. The first author's *P.B.-A.* specimen 638b of *P. tongatensis* (Collins *et al.*, 1899b, as *P. senticulosa*, San Diego, California), although purported to be tetrasporic, is actually a male specimen and the sori agree with the type. Bermuda cystocarps are short-stalked and ovoid with broad ostioles, 220-250 µm in diameter (Fig. 14), while those in one MICH isotype of *P. tongatensis* are morphologically similar and range from 210-300 µm in diameter.

Polysiphonia exilis Harv. 1853: 47
Fig. 15

Type locality: Key West, Florida, western Atlantic.
Collections: Bermuda-*CWS/RBS* 85-1-15, ⊕, 5 June 1985, south of Sinky Bay, southwest end of Bermuda Is., 32° 13.0′ N, 64° 50.5′ W, depth 29 m; *CWS/RBS* 85-18-6, ⊕, 15 June 1985, south of Christian Bay, southwest end Bermuda Is., 32° 13.2′ N, 64° 50.7′ W, depth 27-40 m; *CWS/RBS* 85-19-9, ⊕, 15 June 1985, southwest of Long Bar, west of High Point, Bermuda Is., 32° 13.5′ N, 65° 01.3′ W, depth 30-34 m; *CWS* 96-6-10, 3 July 1996, Devonshire Bay, Bermuda Is., 32° 17.9′ N, 64° 44.7′ W, on littoral rock and algae.

Remarks: *Polysiphonia exilis* was reported from Bermuda during the last century by Dickie (1874), Hemsley (1884), and Murray (1888), but interestingly not by Collins & Hervey (1917) and Howe (1918) in their later, more complete summaries of the flora. Despite W.R. Taylor's extensive work with the Bermuda flora (Schneider & Searles, 1997), there are only two local specimens attributed to *P. exilis* in MICH, both belonging to the same collection from Trott's Pond (*A.J. Bernatowicz* No 49-331), and we find these to be the similar *P. howei* Hollenb. *in* W.R. Taylor (1945).

We have made both inshore and offshore collections which reaffirm the presence of *Polysiphonia exilis* in the Bermudas. In the Devonshire Bay midlittoral, specimens to 3 cm tall were found in the lower yellow zone associated with *Cladophoropsis membranacea* (C. Agardh) Børgesen and *Laurencia papillosa* (C. Agardh) Grev., just below the upper yellow zone where *P. howei* is found as well in a ubiquitous horizontal stratum with *Bostrychia tenella* (J.V. Lamour.) J. Agardh (for zones refer to Stephenson & Stephenson, 1972). All of the deep-water collections of *P. exilis* were epiphytic on *Lobophora variegata*.

The 8-10 periaxial cells of *Polysiphonia exilis* line up in straight longitudinal rows (Fig. 15), while those of *P. howei* (generally 10-12) are offset from segment to segment (Hollenberg, 1968b, figs 1D, 2A, 3C). Axial segments of *P. exilis* are shorter than those of *P. howei*, often less than half as long as broad in both prostrate and erect axes. Erect branches of *P. exilis* arise mostly from the dorsal surface of prostrate axes and rhizoids are cut off from median or proximal positions of ventral periaxial cells (Fig. 15; Hollenberg, 1968b), unlike *P. howei* (radial disposition of branches, distal rhizoids) (Taylor, 1945). Both species develop thicker axes in Bermuda than previously reported elsewhere, *P. exilis* to 230 µm in diameter and *P. howei* to 210 µm in diameter.

Polysiphonia flaccidissima Hollenb. 1942: 783
Figs 16-18

Type locality: Laguna Beach, California, eastern Pacific.
Collections: Bermuda-*CWS/RBS* 83-4-3, 5 Aug. 1983, east of St Catherine's Point, 32° 23.9′ N, 64° 34.3′ W, depth 18-21 m; *CWS/RBS* 83-8-32, 7 Aug. 1983, Jacks Flats, east of St Georges Is., 32° 23.1′ N, 64° 38.0′ W, depth 15-18.5 m; *CWS/RBS* 85-5-10, ♂, 7 June 1985, north of Pilchard Dicks, northwest of Somerset Is., 32° 23.6′ N, 64° 55.0′ W, depth 32 m; *CWS/RBS* 85-15-12, ⊕, 13 June 1985, northeast of Great Head, St Davids Is., 32° 22.8′ N, 64° 36.4′ W, depth 30-34 m; *CWS* 96-4-6, ⊕, 2 July 1996, Coot Pond, Achilles Bay, St Georges Is., 32° 23.2′ N, 64° 40.6′ W, depth 1 m.

Remarks: *Polysiphonia flaccidissima* was found mixed with *P. tongatensis* and others in an algal mat inshore, as well as to a depth of 34 m offshore. All of the specimens found were epiphytic on larger algal species, including *Dictyota*, *Lobophora* and *Ceramium*. Offshore, prostrate axes range from 50-85 µm in diameter and erect axes from 30-60 µm in diameter; in the abundant Coot Pond inshore population, prostrate axes are 110-200 µm in diameter and erect axes are 60-100 µm in diameter. In general, prostrate axial segments are 1-3 times as long as broad and those of erect axes are 1-2 times as long as broad in median segments shortening to half or less as long as broad at the apices. Branches arise in the axils of trichoblasts and are distinctly alternate, the spindle-shaped branchlets often appearing to be pinnate (Fig. 17). Conspicuous scar cells remain after the trichoblasts are lost and rhizoids are cut off from the proximal ends of periaxial cells of prostrate segments (Fig. 16).

Tetrasporangia are formed in short, often broken, spiral series in upper portions of the branches, one per segment, and they are elongate when initiated, mostly swelling to subglobose at maturity and 22-40 µm in diameter by 30-75 µm long. The short series of elongate tetrasporangia are reminiscent of Brazilian plants illustrated by Yoneshigue & Villaça (1986), but unlike long, globose series elsewhere (Kapraun, 1979; Kapraun *et al.*, 1983; Young & Kapraun, 1985). Elliptical spermatangial sori are formed on the basal cells of trichoblasts and are subtended by the trichoblasts (Fig. 18). These sori are 22-48 µm in diameter and 105-125 µm long and mostly lack vegetative tip cells, similar to specimens from Brazil (Yoneshigue & Villaça, 1986). In the Pacific, male sori of *Polysiphonia flaccidissima* are "lanceolate, 30-40 x 150-180 µm, mostly with a tip of 1-3 sterile cells" (Young & Kapraun, 1985). Nevertheless, the Bermudian and Brazilian plants appear to be best associated with *P. flaccidissima* for the present.

Although Womersley (1979) found *Polysiphonia flaccidissima* likely to be conspecific with the Mediterranean *P. sertularioides* (Gratel.) J. Agardh, few have followed his lead and recently Kim & Lee (1996) highlighted differences between them, including cicatrigenous branching in the latter.

Polysiphonia sphaerocarpa Børgesen 1918: 271
Fig. 19

Type locality: Store Nordsidebugt, St Thomas, Virgin Islands, Greater Antilles, Caribbean Sea.

Collections: Bermuda-*CWS/RBS* 83-8-19, ♀, 7 Aug. 1983, Jacks Flats, east of St Georges Is., 32° 23.1′ N, 64° 38.0′ W, depth 15-18.5 m; *CWS/RBS* 85-1-12, ⊕, 5 June 1985, south of Sinky Bay, 32° 13.0′ N, 64° 50.5′ W, depth 31 m; *CWS/RBS* 85-5-37, ♀, 7 June 1985, north of Pilchard Dicks, northwest of Somerset Is., 32° 23.6′ N, 64° 55.0′ W, depth 32 m.

Remarks: Although Bermuda was not included in the distributional range of *Polysiphonia sphaerocarpa* by Taylor (1960), Hollenberg (1968a) mentioned collections from Bermuda by A.J. Bernatowicz which corresponded "closely in most respects with the Pacific specimens, including the enlarged cells on the rim of the pericarp." Hollenberg did not thereafter cite these specimens under the 'material examined' of var. *sphaerocarpa* or his two new varieties of this binomial, but we must assume they belong in the former, a widespread taxon in tropical parts of the Atlantic, Pacific and Indian Oceans. Price & Scott (1992) have since questioned the utility of the varieties in this species. We can affirm the presence of *P. sphaerocarpa* in the Bermudas based upon deep-water epiphytic collections we have made.

This species is initially an erect species, often later becoming decumbent with attaching rhizoids cut off from periaxial cells. In our specimens, unicellular rhizoids are issued from the proximal ends of ventral periaxial cells, similar to plants of Cribb (1983), Yoneshigue & Villaça (1986), Stegenga & Vroman (1988) and Price & Scott (1992). All of these reports, however, are at odds with the distal rhizoids figured for *Polysiphonia sphaerocarpa* by Børgesen (1918, fig. 267a, text explanation). Many other reports of this species, including Hollenberg's (1968a) first note of *P. sphaerocarpa* from the Pacific, only mention that the rhizoids are separate cells cut off from periaxial cells, but not the position on these cells. In all other features and dimensions, the Bermuda specimens fit those illustrated by Børgesen (1918, 1924), including the large ostiolar cells prominently featured by other authors as a key characteristic (Fig. 19).

Spermatangial sori of *Polysiphonia sphaerocarpa* are illustrated as having distinctly inflated vegetative tip cells by Børgesen (1924), but Yoneshigue & Villaça (1986) demonstrate male sori from Brazil without tip cells, and Price & Scott's (1992) Australian sori have a single enlarged tip cell. Male plants have not as yet been located in Bermuda.

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